Changes in Black Cherry Seed Production: Is Stand Age a Factor?

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Abstract - Beginning in the early 2000s, managers and scientists observed a change in seed production and seed crop frequency for *Prunus serotina* (Black Cherry), an ecologically and commercially important species in the Alleghany Plateau region. This study focused on whether older Black Cherry stands are producing less seed than younger stands. We set 3 clusters of 15 seed traps in each of two ~70-year-old (CG70 and KEF70) and two ~110-year-old (CG110 and KEF110) Black Cherry-dominated stands (total of 45 traps per stand). We collected seeds from August through November from 2010 to 2018. We found that seed production varied by stand age interacting with year ($P < 0.01$), and seed production was greater ($P < 0.01$) in the ~110-year-old stands (3.5 million seeds/ha [1.4 million seeds/acre]) compared with the ~70-year-old stands (368,000 seeds/ha [149,000 seeds/acre]) only in 2018. There were no detectable differences in mean seed production over 9 years based on location (CG vs. KEF; $P = 0.27$). This study found no evidence that older stands produce less seed than younger stands.

Introduction

Since about 2000, forest managers have reported that *Prunus serotina* Ehrh. (Black Cherry) seed crops often are poor and erratic, likely contributing to regeneration difficulties in many stands. Black Cherry became a major component (26% of total basal area in inventoried areas) of the Allegheny National Forest (ANF) following late 19th- and early 20th-century harvests. Many stands originated after 1 or 2 partial cuts from 1850 to 1910 followed by clearcutting for sawlogs and chemical wood from 1900 to 1930 (Marquis 1994). This pattern favored the rapid growth of dominant and codominant Black Cherry relative to other species in these mixed stands resulting in a higher proportion of Black Cherry at maturity. As these stands matured, Black Cherry seed was usually abundant, being produced 1 out of every 2 years (Hough 1965, Marquis 1990). Black Cherry seeds remain viable in the forest floor for 3 to 5 years, essentially maintaining a constant seedling supply (Bjorkbom 1979, Marquis 1975).

Black Cherry is shade intolerant, and cherry-dominated stands are typically regenerated using a shelterwood method that increases light while leaving seed-producing trees in place to allow seedling establishment over 3 to 5 years prior to final overstory removal (Nyland et al. 2016). Black Cherry was reliably regenerated in most areas on the Allegheny Plateau until the early 2000s. At the same time, foresters reported less reliable and less abundant Black Cherry seed crops across the unglaciated Allegheny Plateau. Shelterwood cuts were made leaving abundant

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Black Cherry residuals, but new seedlings did not develop in a timely manner. This problem has persisted and many sites previously with abundant Black Cherry are now dominated post-harvest by *Betula lenta* L. (Sweet Birch), *Acer rubrum* L. (Red Maple), and other species.

Reduced seed production has been hypothesized as a reason for observed decreased seedling abundance. Black Cherry seed production has been quantified by past research on the Allegheny Plateau in terms of periodicity and abundance. Grisez (1975) conducted a 7-year study from 1963 to 1969 and found poor seed production until the fourth and fifth years of the study; however, it was noted that there was a high degree of tree-to-tree variability and there was never a total failure in Black Cherry seed production. Major droughts occurred during the study in 1965 and 1966 that may have affected the results (NOAA 2018). Grisez's survey encompassed a large region from Crawford to Potter counties, PA, and utilized 5 to 52 trees depending on the year. Flower and seed crops were rated each year by ocular estimate into 1 of 5 classes from trace/none to bumper, based on an assumed maximum amount of flowers or seeds (Grisez 1975). A major finding from this study was that the relationship between flower crops and seed production was weak, with Black Cherry tending to produce abundant flowers every year but the subsequent development of fruit was often poor (Grisez 1975).

A more quantitative seed production study from 1971 to 1976 at 2 locations in the ANF showed that Black Cherry produced "good" seed crops (~300,000 to 500,000 seeds/acre) about every other year during this period (Bjorkbom 1979). Even in years when Black Cherry seed production was poor, many new seedlings germinated from seed stored in the humus (Bjorkbom 1979). In 1974, a poor cherry seed year, more than 84,000 newly germinated seedlings per acre were observed, and new germinants from humus block samples placed in a greenhouse averaged 252,000 seeds per acre from 1973 to 1976 (Bjorkbom 1979). These results differed from those of Grisez (1975) in that seedling supply from new germinants stored in the forest floor was nearly constant in the forest stands studied in the 1970s (Bjorkbom 1979).

Foresters and land managers have suggested that older Black Cherry trees produce less seed than younger trees (e.g., Hanson et al. 2020). Others have reported the period of maximum seed production for Black Cherry is generally between 30 and 100 years of age (Hough 1965, Marquis 1990). With many stands now in the 90- to 120-year age class, it is hypothesized that seed production will become more variable and less abundant. The objective of the current study was to quantify Black Cherry seed produced annually from 2010 to 2018 in stands of contrasting ages at 2 locations in the ANF. We also assessed stand composition and crown condition to relate these metrics to seed production. To further test the stand-age hypothesis, we quantified seed production in 2 old-growth Black Cherry stands in the Tionesta Scenic and Research Natural Area in 2017. One stand originated after a blow down event in 1872, and the other originated from a blow down in 1808 (Bjorkbom and Larson 1977, Hough and Forbes 1943).

Methods

In 2010, we started seed trapping in the same 2 stands used for the Bjorkbom (1979) seed-production study in the 1970s. Both of these stands were 70 years old at the start of the Bjorkbom study in 1971, so they were ~110 years old at the start of this study in 2010. One stand (elevation 567–573 m [1860–1880 ft]) is located near Cherry Grove (CG) within the Allegheny National Forest (ANF), and the other stand (elevation: 610–628 m [2000–2060 ft]) is part of the Kane Experimental Forest (KEF) (Bjorkbom 1979) (Fig. 1). For comparison, we selected a younger-aged stand near each of these 2 older stands, based on approximate stand age, proximity to the older stands, and the requirement that stand basal area of

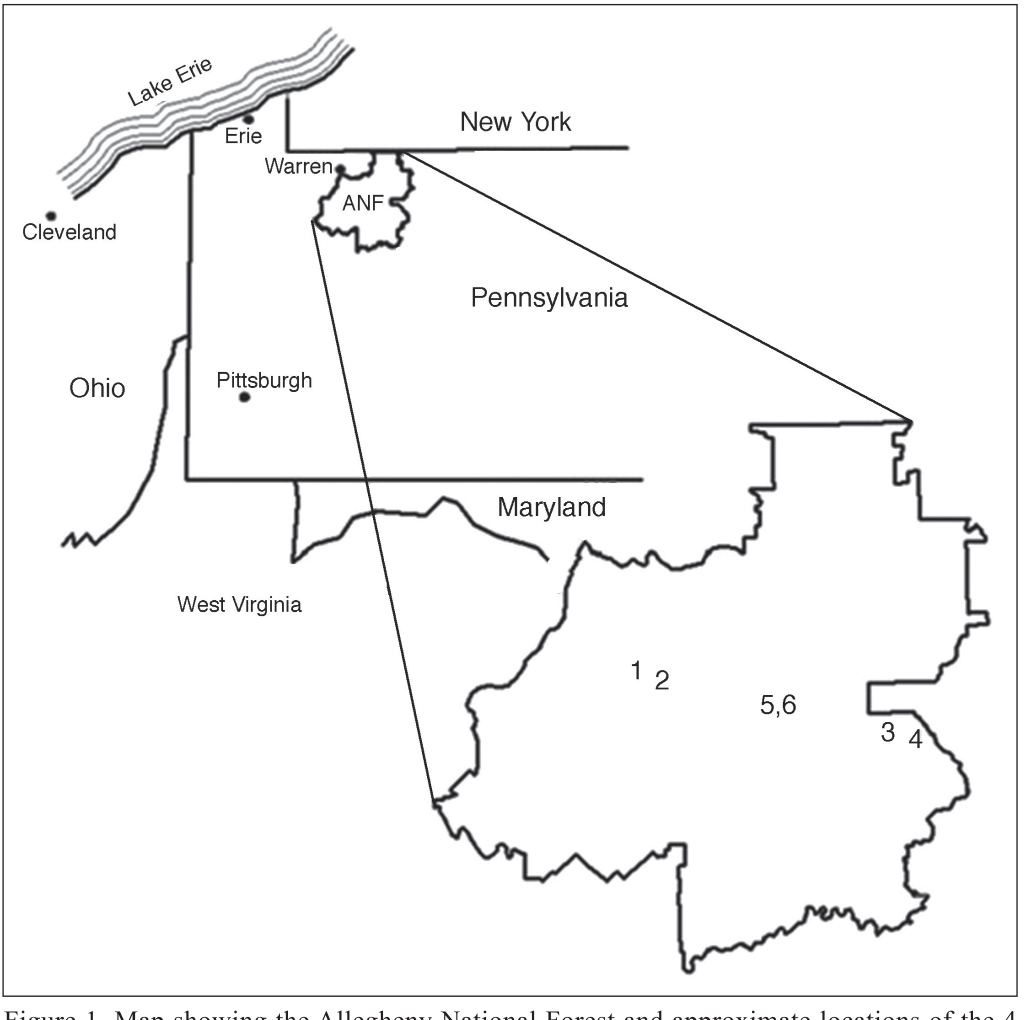

Figure 1. Map showing the Allegheny National Forest and approximate locations of the 4 stands used for seed trapping: 1 = Cherry Grove ~110-year-old stand; 2 = Cherry Grove ~70-year-old stand; 3 = Kane Experimental Forest ~70-year-old stand; 4 = Kane Experimental Forest ~110-year-old stand; 5 = 1872 blowdown origin stand; 6 = 1808 blowdown origin stand.

black cherry was more than 50% of the total stand basal area. Near the older CG stand, we selected a ~70-year-old Black Cherry-dominated stand, where Black Cherry was >50% of the stand basal area (elevation: 576–585 m [1890–1920 ft]) using an ANF stand-age class database. The selected ~70-year-old stand was ~3.2 km (2 mi) southeast of the ~110-year-old stand at Cherry Grove. On the KEF, we selected a ~70-year-old Black Cherry-dominated stand (elevation: 622–628 m [2040–2060 ft]) that had originated as part of a mowing study in 1938. This stand was ~5.6 km (3.5 mi) northwest of the ~110-year-old stand that was originally used by Bjorkbom in the 1970s. All 4 stands are located on top of the plateau with flat or gently sloping topography.

Seed-trapping methods followed Bjorkbom (1979). Seed traps were black plastic pots, ~21.1 cm (8.3 in) in diameter, that we attached 0.9–1.2 m (3–4 ft) off the ground to rebar using zip ties. We positioned 3 clusters of 15 traps in a circular arrangement in each 1.6-ha (4-acre stand). We placed 1 trap in the center of the cluster, 9 traps 18 m (60 ft) from the center trap and at 40 degree intervals around the center trap starting from 360 degrees, and 5 traps 9 m (30 ft) from center trap at 72 degree intervals around the center trap starting at 36 degrees (Fig. 2). Each 15-trap cluster served as a replicate, and we averaged seed trap amounts across the 3 clusters within each stand for mature seed production estimates from August through November.

From 2010 to 2015, we deployed seed traps by 1 August and counted trap contents monthly through 30 November. In 2016 and 2017, we deployed traps earlier in order to assess the amount of flowers and seeds aborted early in the season. In 2016, we set out seed traps on 31 May and collected contents weekly though September and then bi-weekly in October and November. In 2017, we deployed traps on 5 May and collected contents weekly through September and bi-weekly in October and

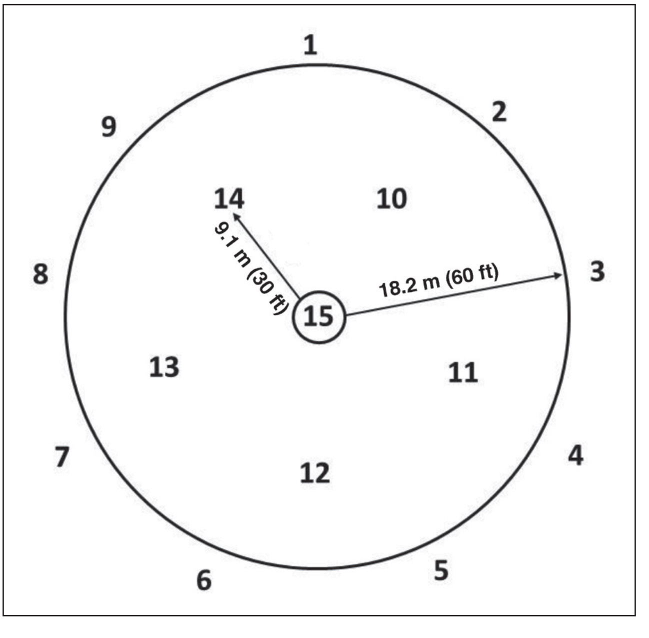

Figure 2. Seed trap positions in each 15-trap cluster. Traps 1–9 are oriented at 40° intervals and 18.2 m (60 ft) from the center trap (15). Traps 10–14 are oriented at 72° intervals and are 9.1 m (30 ft) from the center trap (15).

November. Black Cherry seed is usually mature by August and, for comparisons with Bjorkbom (1979) study, we estimated seed production for the period from 1 August through 30 November in each year.

During 2016, we measured stand composition and tree health in 1.6-ha (0.4-ac) circular plots (radius of 23 m [75 ft]) around each trap cluster using the center trap as the plot center (3 plots in each stand). We assessed species, diameter at breast height (DBH), and crown position (dominant, codominant, intermediate, suppressed) for all standing live trees 12.7 cm (5 in) DBH and larger. We tallied standing dead trees and recorded their DBH. For all the Black Cherry trees in a plot, we estimated the percent live crown ratio (the ratio of live crown length to total tree height expressed as a percent), percent crown density (or amount of light blocked by foliage and branches), and percent fine twig dieback in 5% classes according to Forest Health Monitoring methods (Schomaker et al. 2007). All field personnel received crown-rating training from Forest Inventory and Analysis foresters in May 2016.

We used 2 old-growth stands that originated from blowdown events in 1808 and 1872 in the Tionesta Scenic Area (Sheffield Township, Warren County) to further assess seed production of older Black Cherry trees (Fig. 1). These stands, varying in elevation from ~567 to 585 m [1860 to 1920 ft], are 14.5 km (9 mi) southeast of the CG stands and ~18 km (11 mi) northwest of the KEF stands. We randomly selected 20 Black Cherry trees in each area and placed 2 seed traps beneath the canopy of each tree. This design was used to better estimate the seed production under current stand conditions (dense *Fagus* [beech] brush in some areas and scattered groups of Black Cherry) compared with the previous 15-trap cluster used by Bjorkbom (1979). We deployed the traps on 1 May 2017 and counted contents monthly through 29 November 2017. We evaluated current stand composition and tree health using 20 points established along a 3- chain by 3-chain grid in each approximately 4–6 ha (10–15 ac) stand. We used a 10 basal area factor prism for the assessment of overstory species composition. We measured all trees in the prism plot and evalutated the crown health of Black Cherry trees using the same protocols as described for the ~70- and ~110-year-old stands. Because the traps were not deployed in 15-trap clusters, we artificially clustered the selected trap trees in groups of 7, 7, and 6 trees (14, 14, and 12 seed traps, respectively) to enable calculation of seed production in a manner similar to that for the other stands described above.

Calculations for seed production on a per area basis followed Bjorkbom (1979). This method assumes that Black Cherry crowns cover 0.4 ha (1 ac) and the area of the seed traps is summed and expanded to a 0.4-ha (1-ac) basis. Seed trap counts were summed across the 15 traps in a cluster and then averaged across the 3 clusters in a stand. Each trap is about 0.034 m^2 (0.37 ft^2) and all 15 traps add up to 0.53 m^2 (5.65 ft^2). To express the result on a 0.4-ha (1-ac) basis, the number of seeds is multiplied by 7709 (43,560/5.65). Only seeds produced after August 1 were assumed mature and viable. We considered seeds, flowers, and/or pedicels found in traps in May, June, and July to be immature and/or aborted.

We analyzed the study design for the seed-production data as a repeated-measures nested randomized complete block with year and stand age as fixed effects and cluster within a site by stand age as the random effect. The seed-trap cluster was the experimental unit used for the analyses. We conducted statistical analyses with SAS PROC GLIMMIX (SAS Institute Inc. 2008) using a restricted or pseudo maximum likelihood technique and the Kenwood–Roger correction method for the denominator degrees of freedom (Littel et al. 2006). We assessed normality of the data with the Shapiro–Wilk test and used alternative distributions including the lognormal (with the identity link function) and the gamma distribution (with the log link function) when they best fit the data. Covariance structures used for these repeated measures models included mainly the autoregressive order 1 structure (AR[1]) and the AR(1) with heterogeneous variances (ARH[1]). Model terms were assessed at the $\alpha = 0.05$ significance level. We assessed residuals for normality by plotting and with the Shapiro–Wilk test and evaluated residuals for fixed effects for homogeneous variance using Levene's test. Where appropriate, we used pairwise comparisons with the Tukey–Kramer adjustment with $\alpha = 0.05$ significance to compare least square means of seed production. We used a similar model to test for differences between sites (CG vs KEF).

We evaluated stand health data (from 2016) with respect to stand age using a randomized complete block model with stand age as a fixed effect and site and trap cluster (plot) nested within site as the random effects with SAS PROC GLIMMIX (SAS Institute 2008). We compared mean live crown ratio, crown dieback, and crown density among the sampled stands to evaluate whether there were differences in health status based on stand age. A small or reduced live crown ratio could indicate significant dieback or branches shed in the upper or lower crown. Additional analyses tested for differences in health metrics among each of the 4 stands with stand and plot as fixed effects. We compared least square means of health metrics for each stand using the Tukey–Kramer multiple comparison method.

For the Tionesta old-growth stands, seeds found in traps were counted and summed in each of the 3 seed-trap clusters and then averaged for the respective stands that originated in 1808 and in 1872. We used a fixed-effects analysis of variance to compare seed production and crown health metrics between these 2 old-growth stands.

To compare 2017 seed production in the 2 old-growth Black Cherry stands with seed production in the ~70- and 110-year-old stands, we used a one-way analysis of variance model with stand as a fixed effect to test for differences in 2017 mean seed production among the 5 sites sampled (CG70, CG110, KEF110, T1808, T1872). The KEF70 stand was omitted since no seeds were produced at this site in 2017. We assessed the 2017 seed production data (August to November) for normality and transformed the data when necessary for analyses of variance.

To compare the periodicity and pattern of seed production observed from 1971 to 1976 (Bjorkbom 1979) with the seed production in our study, we calculated unadjusted raw means for 2010 to 2015 for CG110 and KEF110. These were the same stands used in the 1970s. We graphically compared the 1971–1976 seed production and the 2010–2014 seed production data for these 2 stands.

Results

Flower and seed production

Nine years of seed production data show considerable temporal and site variability (Fig. 3). In 2010, the first year of the study, a bumper Black Cherry seed crop was produced with peak mean production (least square means) of 5.7 million seeds/ha (2.3 million seeds/acre) at KEF110. However, since 2010, seed production has

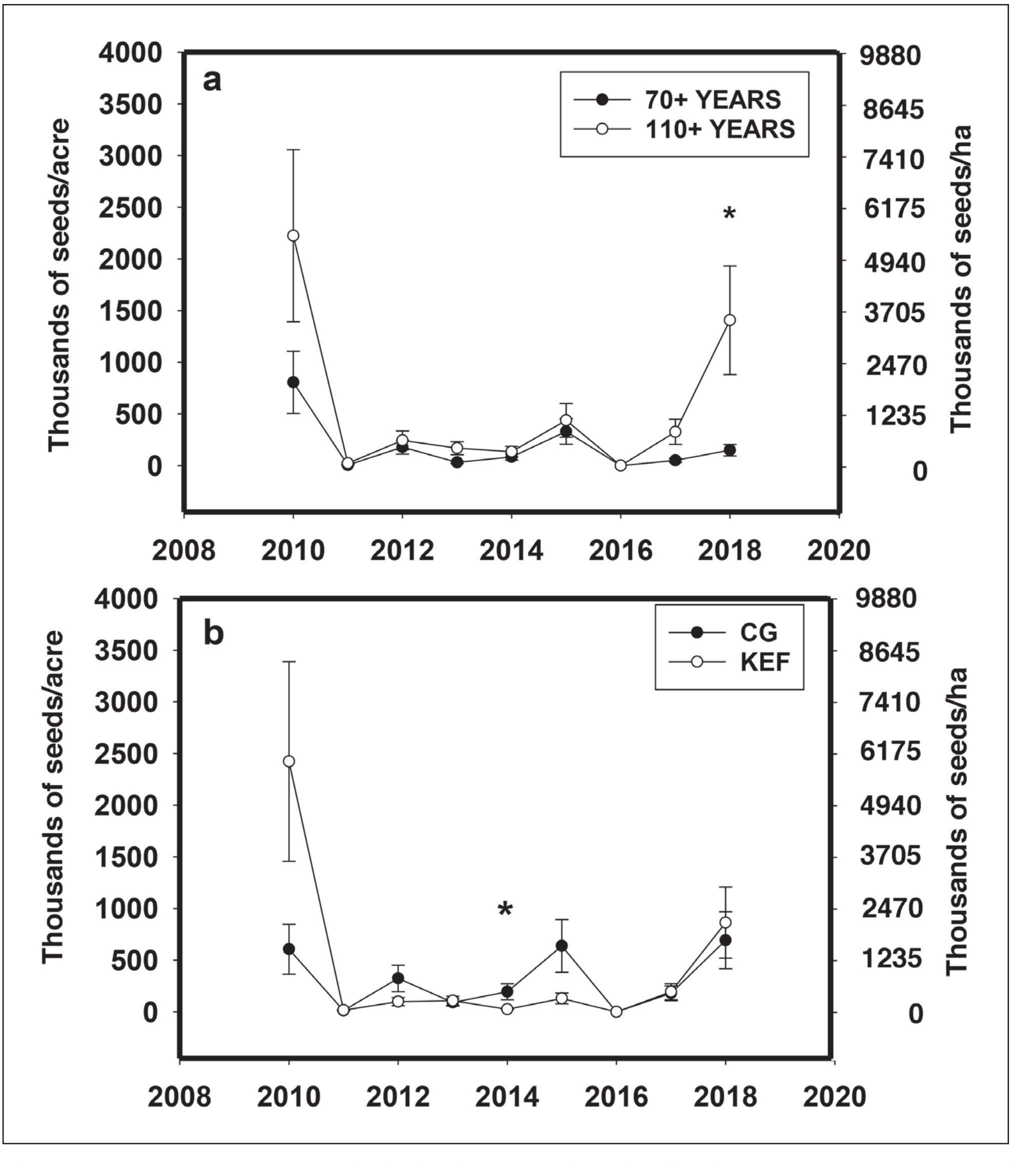

Figure 3. Least square means of Black Cherry seed production from 2010 to 2018 summed from August to November each year: (a) two ~110-year-old stands and two ~70-year-old stands and (b) comparison of seed production between the CG and KEF stands. Asterisks indicate a significant ($P \leq 0.05$) pairwise difference.

been considerably less and only exceeded 988,000 seeds/ha (400,000 seeds/acre) at CG110 in 2015 (1.08 million seeds/ha [437,000 seeds/acre]), and at KEF110 in 2018 (3.5 million seeds/ha [1.4 million seeds/acre]). A significant ($P = 0.012$) interaction of stand age and year required comparisons of individual means by stand age and year (Table 1, Fig. 3a). Pairwise comparisons of ~110- vs ~70-year-old stands showed that the only year when older stands produced significantly ($P = 0.006$) different seed abundance was in 2018 when older (~110 years) stands produced 3.5 million seeds/ha (1.4 million seeds/acre) compared with only 368,000 seeds/ha (149,000 seeds/acre) produced in younger (~70 years) stands.

There were no significant differences ($P = 0.271$) in seed production between the CG and KEF sites (Table 1), but there was a significant interaction of site by year. Tukey–Kramer adjusted pairwise comparisons of least square means by year showed a significant ($P = 0.036$) difference in seed production between CG (479,140, seeds/ha [193,900 seeds/acre]) and KEF (60,300 seeds/ha [24,400 seeds/acre]) in 2014, but no other yearly pairwise differences were significant due to the highly variable data.

There was a significant interaction of stand age by year (Table 1). While there was a significant difference between ~70-year-old and ~110-year-old stands in 2018, there was no significant difference in the amounts of seed produced between ~70- and ~110-year-old stands for the remaining 8 years. The unadjusted raw means show older stands produced 1,401,269 seeds/ha/year (567,074 seeds/acre/year) over 9 years, compared with younger stands that produced an average of 224,600 seeds/ha/year (90,900 seeds/acre/year). Averaged across all 9 years, the KEF110 stand produced the most seed, about 1,842,740 seeds/ha/year (745,730 seeds/acre/year), while the KEF70 stand produced the least amount of seed averaging 351,198 seeds/ha/year (142,125 seeds/acre/year). Aside from the bumper seed crop in 2010, the only other years with a large seed crop were 2015 and 2018. In 2015, only the CG stands produced over 988,420 seeds/ha (400,000 seeds/acre) (Fig. 3). In 2018, both the CG and KEF sites produced over 1,730,000 seeds/ha (700,000 seeds/acre) (Fig. 3b), and most of the seed at both sites was produced in the older stands, KEF110 and CG110.

Seed traps deployed in June 2016 and May 2017 and collected weekly showed large numbers of flowers or developing seed that fell as pedicels (stems that hold

Table 1. *F*-values and associated probability levels for models testing age effects on seed production and site effects on seed production from 2010 to 2018 at 4 sites.

	F-value	Pr > *F*
Age model factor		
Age	19.5	0.001
Year	51.3	<0.001
Age*year	2.8	0.012
Site model factor		
Site	17.2	0.271
Year	45.0	<0.001
Site*year	5.3	<0.001

the flowers to the raceme or putatively aborted flowers), or immature seed into seed traps (Fig. 4) Weekly collections from the seed traps showed that most immature flowers, pedicels, or seeds fell from the racemes in early June in both 2016 and 2017. In June 2017, more than 5.7 million pedicels, aborted flowers, or immature seed per ha (2.3 million per acre) were associated with KEF110 (Fig. 4b). This stand produced the most mature seed in 2017, ~956,00 seeds/ha (387,000 seeds/acre). A similar pattern was observed in 2016, but mature seed was ~684,500 seeds/ha (277,000 seeds/acre) at KEF110 and immature seed, pedicels, and aborted flowers peaked at ~2.7 million seeds/ha (1.1 million per acre) (Fig. 4a).

Stand composition and health

All 4 seed trapping stands were dominated by overstory Black Cherry (Table 2). Black Cherry basal area (live + dead trees) varied from 25.7 m^2/ha (111.8 ft^2/acre)

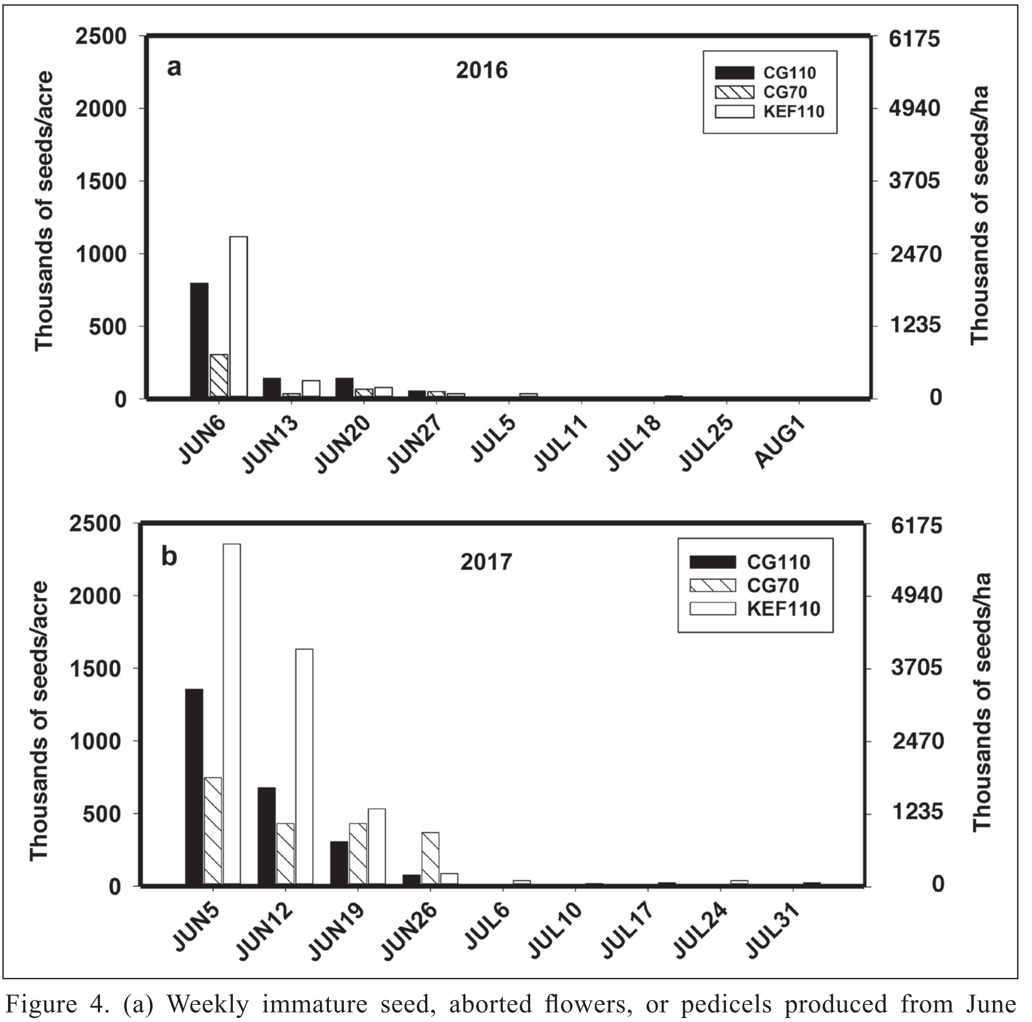

Figure 4. (a) Weekly immature seed, aborted flowers, or pedicels produced from June through July 2016 and (b) weekly immature seed, aborted flowers, or pedicels collected from June 6 through July 2017. None were collected at KEF70 in 2016 or 2017.

in the CG70 stand to 40.7 m^2/ha (177.1 ft^2/acre) at KEF110. The stand with the lowest seed production, KEF70, had an average of 18.3% standing dead Black Cherry basal area or ~5.7 m^2/ha (25 ft^2/acre) averaged across three 0.16- ha (0.4-acre) plots associated with the seed trapping clusters. Of the 189 Black Cherry trees in the 3 plots at KEF70, 71 trees or 37% of the trees were standing dead. Mean diameter of the dead trees at KEF70 was 21.6 cm (8.5 in) (min–max = 12.7–43.4 cm [5.0–17.1 in]). The mean percent standing dead basal area of all other species combined was modest, varying from 2.8% at KEF70 to 13.2% at CG110 (Table 2).

Black Cherry crown health metrics from 2016 did show significant ($P \leq 0.05$) differences related to stand age. Mean live crown ratio was significantly greater (trees had longer/taller crowns), 22%, for ~110-year stands compared with 16% for ~70-year stands. Mean crown density (higher values indicate denser crowns) also differed significantly with mean crown density averaging 30% in ~110-year stands and just 21% in ~70-year stands. Similarly, mean crown dieback, which includes fine twigs <2.54 cm (<1 in) in diameter, was significantly greater in ~70 year stands (18%) compared with ~110 year stands (7%).

Table 2. Total basal area (ba), basal area of Black Cherry (BC), percent standing dead Black Cherry basal area, basal area of all other species combined, and percent standing dead basal area of all other species in the four stands used for seed trapping studies. All basal area data given as mean m^2/ha ± se (ft^2/acre ± se). % basal area dead given as mean ± se.

Site	Total ba	BC ba	% BC ba dead	All other spp. ba[1]	% all other spp. ba dead
CG110	41.0 ± 3.8 (178.8 ± 16.4)	26.0 ± 3.4 (113.1 ± 14.6)	5.9 ± 0.04	15.1 ± 2.2 (65.8 ± 9.4)	13.2 ± 0.07
CG70	44.4 ± 5.4 (193.3 ± 23.3)	25.7 ± 2.7 (111.8 ± 11.8)	11.9 ± 0.02	18.8 ± 4.6 (82.0 ± 19.9)	6.5 ± 0.03
KEF110	56.0 ± 3.9 (243.7 ± 16.9)	40.7 ± 6.3 (177.1 ± 27.4)	7.2 ± 0.03	15.3 ± 3.9 (66.6 ± 17.0)	4.1 ± 0.04
KEF70	46.5 ± 3.2 (202.4 ± 14.0)	31.8 ± 0.4 (138.5 ± 1.7)	18.3 ± 0.05	14.7 ± 3.4 (63.9 ± 14.7)	2.8 ± 0.03

[1]Includes: *Acer saccharum* Marsh. (Sugar Maple), Red Maple, American Beech, *Betula alleghaniensis* Britton (Yellow Birch), Sweet Birch, *Tsuga canadensis* (L.) Carrière Eastern Hemlock), *Liriodendron tulipifera* L. (Yellow Poplar), *Fraxinus americana* L. (White Ash), *Acer pensylvanicum* L. (Striped Maple), and *Magnolia acuminata* (L.) L. (Cucumbertree).

Table 3. Least square means (standard error) of Black Cherry crown vigor, live-crown ratio, fine-twig dieback, and crown density in 4 stands used for seed trapping. Means in a column with the same letter were not significantly different ($P > 0.05$) using the Tukey–Kramer multiple comparison adjustment.

Site	% live-crown ratio (se)	% dieback (se)	% density (se)
CG110	23.1 (0.5) a	8.0 (2.4) a	28.9 (0.8) a
CG70	17.3 (0.5) b	13.1 (3.4) ab	23.5 (0.7) b
KEF110	21.0 (0.2) a	6.9 (0.4) a	30.4 (0.6) a
KEF70	14.4 (0.7) c	23.6 (2.2) b	19.2 (0.4) c

Analyses of tree-health metrics based on comparisons among the 4 individual stands highlights considerable variation in crown-health conditions among the 4 seed-trapping sites (Table 3). At KEF70, Black Cherry trees, on average, had smaller live-crown ratios, 14.4%, and lower crown density, 19.2%, both significantly less than in the other 3 stands (Table 3). Fine twig dieback was also highest at KEF70, averaging 23.6%, while KEF110 had the least amount of fine twig dieback, averaging 6.9%. Crown density was significantly greater at both CG110 and KEF110 than at KEF70 and CG70 (Table 3).

Tionesta old-growth stands

Both of these old-growth stands produced seed in 2017, the single year that they were sampled. The older stand that originated from an 1808 blow down produced the most seed, averaging 3.63 million seeds/ha (1.47 million seeds per acre), compared with the stand originating in 1872 that produced an average of 961,000 seeds/ha (389,000 seeds per acre) in the period from August through November. Statistical comparisons of these means shows that the 1808 origin stand had a marginally significantly ($P = 0.097$) larger seed crop from August to November compared with the 1872 origin stand. It should be noted that these seed production estimates are biased upward compared with those in the ~70- and ~110-year-old stands because the traps in the old-growth stands were placed directly below Black Cherry crowns whereas traps in the other stands were positioned systematically and may not have been directly under a Black Cherry crown.

Similar to the ~70- and ~110-year-old stands, a large number of flowers and seeds failed to develop in the period from May to the end of July (Fig. 5). The peak

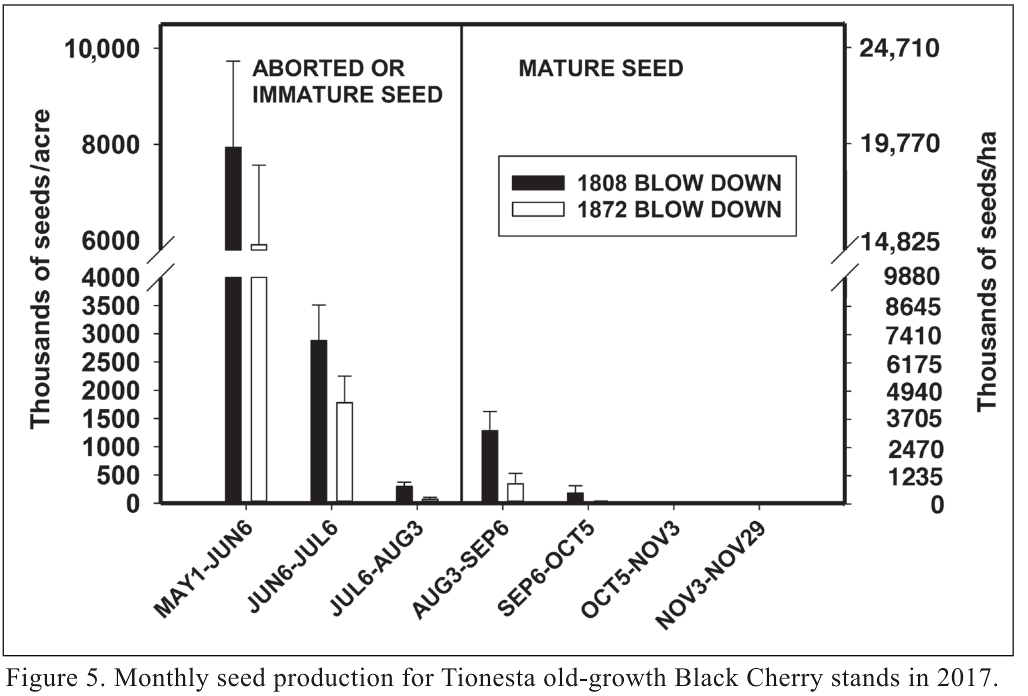

Figure 5. Monthly seed production for Tionesta old-growth Black Cherry stands in 2017.

months when empty pedicels and aborted seeds were collected were May and June, with the 1808 origin stand having almost 20 million aborted flowers, seeds, or empty pedicels per ha (8 million per acre) in May. However, this stand went on to produce a large mature seed crop from August through November as described above.

Black Cherry and *Fagus grandifolia* Erhr. (American Beech) were the dominant species in each stand, comprising more than 50% of the stand basal area. The 1872-origin stand had an average of 15.8% standing dead Black Cherry basal area compared with 12.5% in the 1808-origin stand (Table 4). Crown-health variables indicated not a lot of difference between the 2 stands (Table 5). The live-crown ratio was significantly ($P \leq 0.05$) greater, 28.8%, in the older, 1808-origin stand compared with 24.9% in the younger, 1872-origin stand. Mean crown density and dieback were not significantly different between the 2 stands. There was no apparent defoliation from the moth *Rheumaptera prunivorata* Ferguson (Cherry Scallop Shell) in these stands in 2017.

Table 4. Total live and dead basal area (ba), basal area of Black Cherry (BC), percent standing dead Black Cherry basal area, basal area of all other species combined, and percent standing dead basal area of all other species in the 2 old growth Black Cherry stands in the Tionesta Scenic Area (based on 20 prism plots in each stand). All basal area data given as mean m^2/ha ± se (ft^2/acre ± se). % basal area dead given as mean ± se.

Site	Total ba	BC ba	% BC ba dead	All other spp. ba[1]	% all other spp. ba dead
1808 origin	36.3 ± 1.5 (158.0 ± 6.7)	10.0 ± 1.5 (43.5 ± 6.5)	12.5 ± 3.6	26.3 ± 1.7 (114.5 ± 7.5)	10.8 ± 2.4
1872 origin	33.3 ± 1.5 (145.0 ± 6.5)	12.6 ± 1.5 (55.0 ± 6.5)	15.8 ± 5.3	20.7 ± 1.3 (90 ± 5.7)	13.5 ± 2.7

[1]Includes same species as listed in Table 2.

Table 5. Differences in mean live-crown ratio, crown dieback, and crown density at the 2 old-growth Black Cherry stands in the Tionesta Scenic Area. Means with a different letter in a column are significantly different ($P \leq 0.05$).

Stand	% live-crown ratio (se)	% crown dieback (se)	% crown density (se)
1808 Origin	28.8 (0.9)a	7.1 (0.4)a	35.7 (1.2)a
1872 Origin	24.9 (1.2)b	8.3 (0.7)a	34.4 (0.8)a

Table 6. Least square means of Black Cherry seed production (in thousands of seeds per ha ± se [per acre ± se]) for mature seeds collected at 5 sites from August through November 2017. The KEF70 site was omitted since no seed was produced in 2017. Means with the same letter are not significantly different ($P > 0.05$) using the Tukey–Kramer multiple comparison adjustment.

Site	LSmean
1808 origin	3994.0 ± 1025.0 (1617.7 ± 4150)a
KEF110	1027.0 ± 247.9 (415.6 ± 100.3)b
1872 origin	818.4 ± 198.2 (331.2 ± 80.2)b
CG110	547.3 ± 132.5 (221.5 ± 53.6)bc
CG70	238.7 ± 57.1 (96.6 ± 23.1)c

While there were differences in seed-trapping methodology making comparisons less than ideal, analyses of mean seed production among the 5 stands that produced seed in 2017 showed that the 1808-origin stand at Tionesta had a significantly larger crop than was produced at the CG110 and CG70 sites (Table 6). The seed produced at the 1808-origin stand was almost 4 times greater than the amount produced at KEF110 and the 1872-origin stand. These comparisons should be interpreted with care since the trapping methodology likely caused more seeds to be captured at the Tionesta stands.

Discussion and Conclusions

These results indicate that ~110-year-old Black Cherry stands produce as much as ~70-year-old stands, and there is no evidence of decreased seed production with increased stand age over the 9 years from 2010 to 2018. While there was no statistically significant difference in seed production between ~70- and ~110-year-old stands overall, the ~110-year-old stands produced significantly more seed than ~70-year-old stands in 2018. There is only 1 year of data from the Tionesta old-growth stands, but it is clear that these stands produced large amounts of seed in 2017. The older stand that originated from an 1808 blow down had the largest seed crop of any stand studied in 2017. Notably, Hough (1960) reported that Black Cherry stands as old as 180 years still produced viable seed.

The older ~110-year-old stands may produce more seed because of larger and deeper crowns and possibly more leaf area. Crown-health metrics show that Black Cherry trees in the ~110-year-old stands had significantly greater ($P < 0.05$) live-crown ratios than Black Cherry trees in ~70-year-old stands. Similarly, ~110-year-old stands had greater ($P < 0.05$) crown density (more branches and foliage based on an ocular estimate) compared with crown density in ~70-year-old stands (Table 3).

Comparisons of contemporary seed production with the Bjorkbom data from the 1970s highlights the changes in the periodicity of seed production (Bjorkbom 1979). During the 1970s, Black Cherry seed production usually varied with a "good" year followed by a "poor" year (Bjorkbom 1979). Additionally, Marquis (1990:597) noted that on the Allegheny Plateau of northwestern Pennsylvania, good seed crops of Black Cherry occurred "about every other year". From the Bjorkbom (1979) study, both the CG and KEF stands produced >740,000 seeds/ha (>300,000 seeds/acre) in 3 out of 6 years. From the contemporary data, 3 of the 4 stands produced >740,000 seeds/ha (>300,000 seeds/acre) in 3 out of 9 years, and the fourth stand (KEF70) produced that many seeds only in 2010. The "bumper" seed crop in 2010 tends to skew upward the mean seed production average from 2010 to 2018 for all 4 stands. However, there is little indication of a periodicity of seed production from 2010 to 2018 that is comparable to that noted in Bjorkbom's (1979) study from 1971 to 1976 (Fig. 6). Using unadjusted raw means (not the least square means), the CG110 stand shows some indication of periodic seed production with a second large seed crop in 2015; however, seed production was poor in 2016 and 2017 (Fig. 3). The KEF110 stand does not have any pattern of periodic seed production through 2018.

Neither of the younger stands, CG70 and KEF70 showed indications of periodic seed production similar to the Bjorkbom (1979) 1970s results.

During the study, several disturbance events occurred that did not uniformly affect the different sites. Both the CG70 and CG110 stands had minimal disturbances during the study. The KEF70 site experienced several insect defoliations starting with a *Hyphantia cunea* (Drury) (Fall Webworm [FWW]) infestation in 2012. This

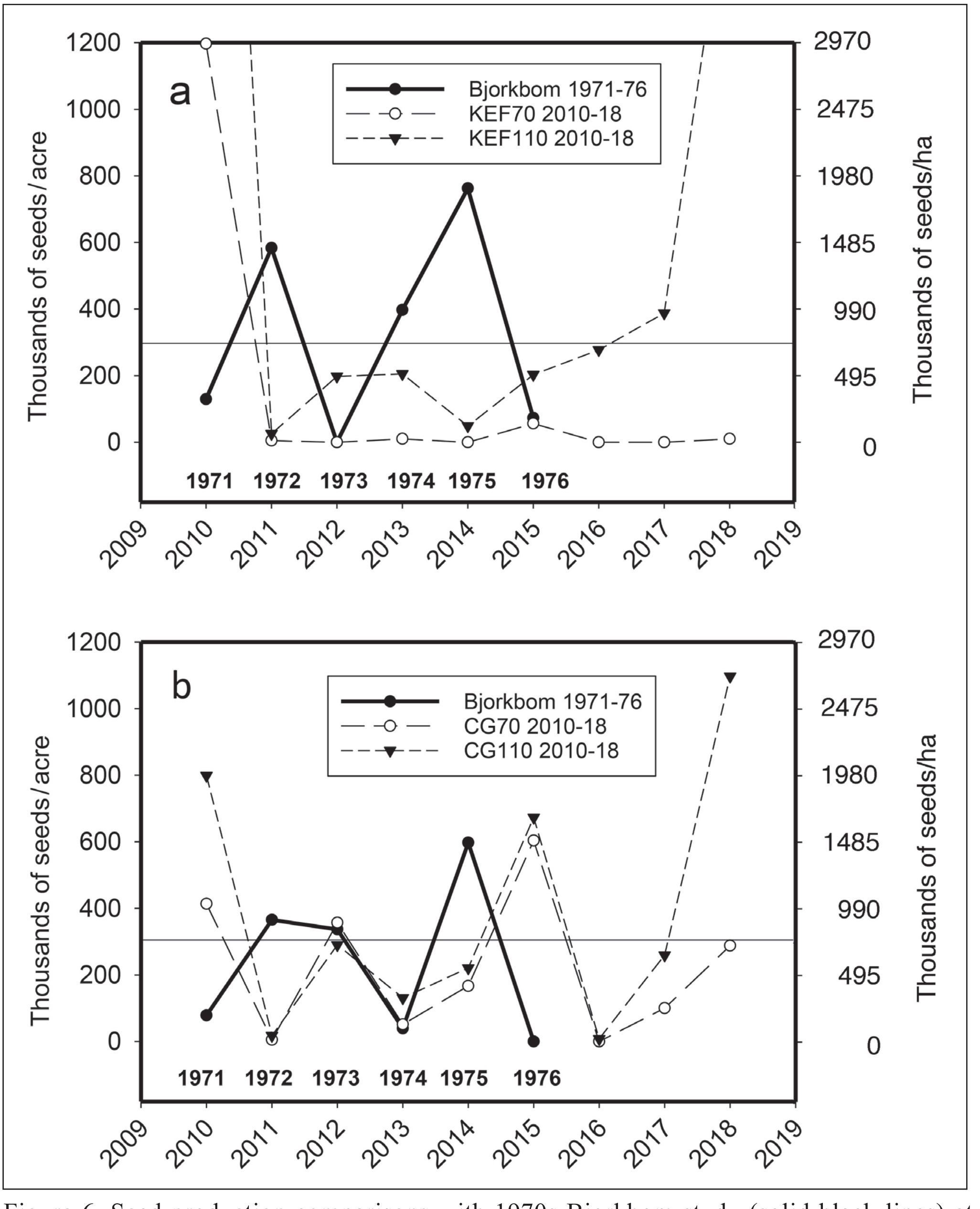

Figure 6. Seed production comparisons with 1970s Bjorkbom study (solid black lines) at (a) KEF and (b) CG stands. At KEF data are beyond the *y*-axis so hidden for 2010 and 2018.

late-season defoliator affected the trees at KEF70, but not at any of the other 3 sites in 2012. In 2013, the KEF70 trees had very light infestations from FWW. In 2014, there was a very light infestation of the Cherry Scallop Shell moth (CSSM) at KEF70, but not at any of the other 3 sites. CSSM is a mid-season defoliator that primarily attacks Black Cherry by causing injury and defoliation by late July or early August. In 2015, the KEF70 trees were heavily defoliated by CSSM, but there was variation in the degree of defoliation, with some trees totally defoliated and others just moderately to lightly defoliated. In 2016, the KEF70 Black Cherry trees were again heavily defoliated by CSSM. The KEF110 Black Cherry trees had only light infestations of CSSM in 2015 and 2016, and the CG70 and CG110 stands were unaffected by CSSM during this time. By 2017, the CSSM infestation had diminished significantly, and there was little to no defoliation at any of the seed-trapping sites. These defoliations at KEF70 likely account, at least in part, for the poor crown condition and poor seed production at this site.

There are several hypotheses about factors that impact Black Cherry seed production. These involve climate change, erratic weather, and decreases in forest pollinators. Examination of decadal precipitation and temperature means since the 1950s for Warren and McKean counties, showed that April–July mean minimum temperatures have increased since the 1990s compared with mean minimum temperatures from the 1950s to 1980s (NOAA 2018; S. Stoleson, USDA Forest Service, Northern Research Station, Irvine, PA, pers. comm.). No other significant changes in temperature or precipitation means were found for the period from 1950 to 2015.

Black Cherry typically flowers starting in early to mid-May and continuing into early June. There is considerable year-to-year and tree-to-tree variability in time of flowering. Late-spring frost events are common on the Allegheny Plateau and frequently coincide with Black Cherry flowering. Freezing or below-freezing temperatures were recorded for Warren, PA, in 2010 (May 10–11), 2012 (May 1), 2013 (May 13–15), 2014 (May 5–6), 2015 (May 23), 2016 (May 16), and 2017 (May 8–9) (NOAA 2018). It is difficult to assess the impact of these freezing events on flower and seed production. A study with *Prunus avium* L. (Sweet Cherry), under controlled conditions showed that even without any external indications of injury, internal damage of the style, ovary, and/or stamens may occur due to cold temperatures while the sepals and petals continue their development (Matzneller et al. 2016).

Erratic weather is an additional factor that can compound the impact of frost damage affecting Black Cherry flower and seed production. For example, in March 2012, there was an extended warm period starting about 12 March and continuing to about 26 March with above-average temperatures including readings of 80 degrees on 22 March, 82 degrees on 23 March, and 83 degrees on 24 March. This warm period accelerated Black Cherry flower development with many trees initiating flowering in April of 2012. Freezing temperatures are common in April and occurred frequently in 2012 with the lowest temperatures, 26 degrees, on April 7 and 8. Overall, seed production was poor in 2012 at all 4 stands, with CG70 producing the most seeds 882,000 seeds/ha (357,000 seeds per acre; Fig. 3).

Black Cherry may also produce more flowers and seeds than can be carried to maturity. Other research with *Prunus cerasus* L. (Sour Cherry) reported that 50–75% of blossoms fail to develop and blossoms are dropped in 3 distinct waves unrelated to cold or freezing temperatures (Bradbury 1929). Dissection of aborted fruits in that study showed most flowers had been pollinated, but ovules were shriveled indicating some other factor affected ovule viability. On average, 95% of total blossoms were pollinated in sour cherries so that fruit drop was not due to poor pollination. The author hypothesized that poor nutrition was the primary causal factor affecting pollination success (Bradbury 1929). We documented flower abortions for Black Cherry in 2016 and 2017, during which large numbers of putatively empty pedicels were found in seed traps in late May and early June. Given that both 2016 (May 16) and 2017 (May 8–9) had freezing temperatures during flowering (NOAA 2018), it is possible these could have affected ovules, but there are no conclusive data to prove this as a causal factor. There are no data that report a normal rate of flowering success or failure for Black Cherry.

Other factors potentially affecting Black Cherry flower and seed production are less quantifiable, such as wind and rain events. These occurred in several years during the course of this study and resulted in flowers and developing seeds being stripped from the raceme stem or peduncle. On many trees observed in the field, only bare peduncles or peduncles with only a few remaining seeds were noted. This mechanical injury may play a major role in reducing seed crops, depending on the incidence and severity of the wind and rain events.

Black Cherry is dependent on insect pollinators (Grisez 1974). There is widespread concern about decreasing numbers of pollinating insects mainly affecting agricultural crops (Koh et al. 2016). The importance of insect pollinators in forest ecosystems is widely appreciated but poorly understood. Recent research has shown that early successional habitat and small openings favor more diverse and abundant bee communities compared with mature forest (Roberts et al. 2017). In the southeastern US, thinning combined with shrub control improved bee habitat and thereby increased the abundance and diversity of forest pollinators (Hanula et al. 2015). The closed-canopy nature of the stands in this study along with the development of a dense beech brush understory could negatively impact pollinator abundance and diversity in these Allegheny hardwood stands, but more research will be needed to assess the importance of pollinators on cherry seed production.

A critical missing component of the seed-trapping studies is a seed-viability assessment. Older stands appear to produce more Black Cherry seeds than younger stands, though the differences are not statistically significant. However, a key factor, seed viability, has not been tested. In terms of regeneration, it is really the number of viable seeds rather than just the total number of seeds produced that is relevant. Additional research should assess the seed viability in young and old stands or assess seedling regeneration in stands similar to the work Bjorkbom (1979) did in the 1970s.

The challenges associated with Black Cherry management have accelerated in the 2000s. Inventory data shows that Black Cherry mortality has increased in many parts of Pennsylvania (PA Bureau of Forestry 2015). Regeneration has decreased within the Allegheny National Forest and surrounding region, which led to speculation regarding seed production and stand age. Overall, based on this 9-year study, ~110-year-old stands produced as much seed as ~70-year-old stands in 8 out of 9 years, and in the other year produced more seed than the younger stands. These results indicate stand age is not a major factor affecting seed production.

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